



Norwegian University of
Science and Technology

Habitat characteristics and small-scale variation in life history traits of a large herbivore

Siri Hånes Langen

Biology

Submission date: May 2018

Supervisor: Vidar Grøtan, IBI

Co-supervisor: Ivar Herfindal, IBI
Erling Solberg, NINA
Christer Moe Rolandsen, NINA

Norwegian University of Science and Technology
Department of Biology

Abstract

Identification of habitat characteristics shaping small-scale variation in life history traits is important for our understanding of the magnitude of small-scale resource utilisation for different life history traits. Based on data collected from 74 hunting units in two municipalities in central Norway, I examined geographical variation in two life history traits of moose, early-life body mass based on carcass mass of calves and yearlings shot during the autumn hunt and twinning rate from hunter observations. Spatial variation in these life history traits was subsequently analysed to determine the most important habitat characteristics influencing life history traits. Additionally, I investigated whether there was a trade-off between offspring quantity and quality, and whether this influenced the habitat-performance relationship for the different life history traits. Both early-life body mass and twinning rate exhibited spatial variation and there was positive covariation between these traits. The presence of agricultural areas in the hunting units was found to be the most important habitat characteristic, and both yearling body mass and twinning rate was positively related to the proportion of agricultural areas in the hunting units. This was most likely due to the high abundance of plants with high nutritional status in such areas. In contrast, the life history traits in general, and calf carcass mass in particular, were negatively related to the proportion of habitats assumed to be of poor nutritional quality. Accounting for the effects of habitat characteristics, the calf body mass was not related to twinning rate. This indicate that females in good habitats produce twins at a higher rate, and that these also become large the following autumn. However, the data did not allow to test whether the higher autumn body mass of calves in good areas with a high twinning rate was caused by larger birth weight or a higher growth rate from birth to autumn. The results indicate that geographical variation in habitat composition can explain small-scale variation in life history traits and that especially agricultural areas are important for early-life body mass and twinning rate. However, the trade-off between offspring quantity and quality seems to weaken the habitat-signal on calf body mass.

Sammendrag

Identifisering av hvilke habitatkarakteristikker som skaper småskala variasjon i livshistorietrekk er viktig for å forstå hvordan dyr utnytter ressurser og betydningen det har for ulike livshistorietrekk. Basert på data samlet fra 74 jaktfelt i to kommuner i Midt-Norge har jeg undersøkt geografisk variasjon i to livshistorietrekk hos elg, vekt tidlig i livet basert på kalve- og åringsvekter hos elger som ble skutt under ordinær jakt, og tvillingrate fra sett-elg statistikk. Romlig variasjon hos disse livshistorietrekkene ble deretter analysert relatert til habitatkarakteristikker som tidligere har vist seg å være viktige for elgens bruk av landskapet. I tillegg har jeg undersøkt om det er en avveining mellom antall og størrelse hos avkom for reproduserende elgkyr, og om dette påvirket i hvilken grad habitat kan forklare variasjon i de ulike livshistorietrekkene. Det var stor geografisk variasjon i både vekt tidlig i livet og tvillingrate, og de ulike livshistorietrekkene samvarierte positivt. Landbruksområder var den totalt sett viktigste habitatkarakteristikken, og både åringsvekter og tvillingrate var positivt forbundet med andelen landbruksområder i jaktfeltene. Dette skyldes antagelig at slike områder har mye planter med høyt næringsinnholdet. Det var generell negativ sammenheng mellom andel av habitattyper som ble antatt næringsfattige, og livshistorietrekkene, og spesielt kalvevekt. Når jeg tok høyde for effekten av habitatvariablene, var det ikke signifikant effekt av tvillingrate på kalvevektene, noe som indikerer at i områder som er å anse som gode, produserer voksne kyr oftere tvillinger, og at disse tvillingene også vil være store den påfølgende høsten. Resultatene tyder på at geografisk variasjon i habitat kan forklare småskala variasjon i livshistorietrekk, og at spesielt landbruksområder er viktige for vekten tidlig i livet og tvillingrate. Det virker imidlertid som om avveiningen mellom antall og størrelse på avkom fører til en svakere sammenheng mellom habitat og kalver.

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1. Introduction

In long-lived iteroparous species, temporal and spatial variation in environmental conditions cause individual variation in life-history traits such as growth, survival, fecundity and migration patterns (Sæther 1997, Herfindal et al. 2006a, Herfindal et al. 2006b, Grøtan et al. 2009, Sinclair et al. 2011, Rolandsen et al. 2016). Access to basic physiological needs like water (Hawkins et al. 2003), quantity and quality of forage (Van der Wal et al. 2000), cover and shelter from harsh weather and predators (Conradt et al. 2000, Rettie and Messier 2000, Bjørneraas et al. 2012), and the availability of suitable mates (Clutton-Brock and McAuliffe 2009) are all factors that may cause variation in individual fitness (Gaillard et al. 2000b, Pettoirelli et al. 2001). An individual's home range is expected to contain a variety of habitat types to meet the demands listed above. The home range is often positively related to the animal's size dependent metabolic rate (McNab 1963), and is found to adjust according to individual body size (Harestad and Bunnell 1979, Ofstad et al. 2016). In heterogeneous landscapes, the physiological needs may be fulfilled within small areas due to access to a variety of habitat types within reasonable proximity (Dussault et al. 2005).

Body mass is a key life history trait in many species, such as ungulates (Gaillard et al. 2000b), and is often found to be positively related to survival, mating success and fecundity (Sæther and Haagenrud 1985a, Bérubé et al. 1999, Gaillard et al. 2000b, Garel et al. 2009). Low weights of young individuals may have long-term negative fitness consequences (Lindström 1999, Solberg et al. 2008, Pigeon et al. 2017), and it is usually found that the earlier an individual's development is disturbed, the stronger are the effects (Desai and Hales 1997, Pigeon et al. 2017). The ability to compensate for a small juvenile body weight later in life depends on the environment and possibly sex, since male adult body mass sometimes is found to be more influenced by environmental conditions than female body mass (Solberg et al. 2004). High juvenile weights, increases the probability of higher life-time reproductive success (Pettoirelli et al. 2002). There is often a positive relationship between a mother's size and the size of her offspring (Sæther and Haagenrud 1985b, Gaillard et al. 1992, Nygrén 2003). Paternal condition can also reflect phenotypic condition and contribute to the offspring's quality (Clutton-Brock et al. 1986). Mammalian species often exhibit various types of extensive parental care (Lloyd 1987), whereas ungulates usually only perform maternal care, including pre- and post-weaning care that may lead to variation in early-life body mass (Clutton-Brock et al. 1983, Sheldon et al. 2004, Therrien et al. 2007). Even small differences in forage quality during foraging can have great effects on early-life body mass

and adult body mass, due to the multiplier effect (White 1983, Van der Wal et al. 2000). The multiplier effects is when animals forage selectively, and even small changes in quality or amount of forage intake greatly enhance animal weight gain over time (White 1983). Access to high-quality forage is important for early-life and adult weight gain (Van der Wal et al. 2000, Månsson et al. 2007). In some species, such as the moose (*Alces alces*) foraging conditions during summer has been found more important than winter conditions for early-life body mass (Herfindal et al. 2006b). One of the first life history traits influenced by environment and density-dependent factors is juvenile body mass (Mysterud 2006), as calves and yearlings of ungulates are usually not reproducing, they are most directly influenced by environmental variation in time and space.

Several species are physiologically able to produce multiple offspring per reproductive event, and their fitness will depend on the number of offspring surviving until maturity (Lloyd 1987). However, there is a trade-off between the size and number of offspring (Smith and Fretwell 1974). K-selected species are in general long-lived and iteroparous, and the reproductive effort must be balanced over the expected lifetime to maximise reproductive success (Pianka 1970). Producing multiple offspring is costly, and can be limited by several factors such as age, if correlated with physiological constraints, and environmental conditions, if it affects female condition, and hence, her ability to produce offspring later in life (Nygrén 2003, Garel et al. 2009).

Several previous studies have identified factors causing geographical variation in life history traits at large spatial scales between population (Sand et al. 1995, Gaillard et al. 2000b, Bjørneraas et al. 2009, Garel et al. 2009, Herfindal et al. 2009). Few studies have explored such patterns at a small spatial scale within a population (see e.g., McLoughlin et al. 2007, Allen et al. 2017). Moreover, few studies have examined multiple life history traits simultaneously, and accordingly not explored how life history trade-offs may affect the observed spatial patterns of traits in a population. As a result, there is little knowledge regarding the extent to which small-scale geographic variation in habitat characteristics can explain small-scale variation in life history traits. This includes which habitat characteristics are most influential for specific life history traits, and to what extent trade-offs between offspring quantity and quality affects the habitat performance relationship for the different life history traits.

The moose is a long-lived and large herbivore with a wide geographical distribution in boreal forests of Europe, Siberia and North America (Andersen et al. 1996). During the year, the moose undergo a weight cycle where it gains weight during summer and autumn, and

normally loses weight during the more challenging winter (Hjeljord and Histøl 1999). Moose body growth depends on density dependent and – independent factors, of which the latter includes direct environmental affects (e.g. snow depth) on weight loss as well as indirect environmental effects on plant quality and quantity (e.g., by summer temperature and precipitation, length of growing season Bø and Hjeljord 1991, Herfindal et al. 2006b). In moose, body mass is a key factor affecting age at first reproduction and twinning rate (Sæther and Haagenrud 1983, Markussen et al. 2018), and understanding factors affecting body mass variation is therefore central for understanding variation in vital rates, determining moose population dynamics (Sæther 1997).

The moose have been found to select habitat types which provide both good forage and cover (particularly reproducing females Bjørneraas et al. (2011), and associated with low human activity (Herfindal et al. 2009). However, several human-influenced habitat types are also found to be preferred by moose, like young forest stands and agricultural areas, especially during the summer (Bjørneraas et al. 2011). Accordingly, habitat selection and availability can affect both individual reproductive success (Allen et al. 2017), as well as population growth (Bjørneraas et al. 2012). The habitat composition affects the home range size, where moose residing in low-quality areas usually have larger home ranges than moose residing in high-quality areas (Rolandsen et al. 2010). Within the summer home range, moose select for preferred foraging species, especially leaves from birch (*Betula spp.*) and bilberry bushes (*Vaccinium myrtillus*) (Wam and Hjeljord 2010a, b). Moose are either resident or migratory, of which migratory moose are found to have higher reproductive performance than the resident moose (Rolandsen et al. 2016).

Here, I analyse geographic variation in two life history traits (early-life body mass and twinning rate) in moose at a fine spatial scale, in relation to habitat characteristics that may be important for how moose utilise the landscape, e.g., (Herfindal et al. 2009, Bjørneraas et al. 2011). Data are based on hunter reports of carcass mass of calves and yearlings, as well as an index of twinning rate derived from the sex and age of moose seen during hunting in 74 hunting units across two municipalities in central Norway. I specifically address the following questions: 1) is there spatial variation in body size and fecundity, and to what extent are there a trade-off between quantity and quality of offspring (i.e., are calves smaller where the twinning rate is higher)?, 2) can these potential spatial patterns be explained by variation in habitat characteristics, and are the similar habitat characteristics important for early-life body growth and fecundity?, 3) does of trade-offs between offspring quantity and quality affect the habitat-performance relationship for the different life history traits?

2. Material and methods

2.1 Study area

The study area consists of the municipalities of Stjørdal and Meråker in central Norway (Fig. 1). The study area is within the boreal and alpine vegetation zones, with Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), and downy birch (*Betula pubescence*) dominating in the forest (Moen 1999). Grey alder (*Alnus incana*), aspen (*Populus tremula*), rowan (*Sorbus aucuparia*) and goat willow (*Salix caprea*) are also common (Moen 1999). The study area has a gentle elevational gradient from the fiord of Trondheim to the alpine zone, and especially Meråker municipality consists of large areas above the treeline at 600-700 m. asl. (Moen 1999). There are two densely human populated areas, the towns of Stjørdal and Meråker, however most people live outside these centres (Statistics Norway, www.ssb.no). Agriculture is important in both municipalities, but the intensity of farming decrease with increasing elevation. Grain production dominates the areas at low elevation, where summers are relatively long and warm. At higher elevation where the summers are shorter and colder, the production is mainly grass for livestock (Stokstad and Puschmann 2011). Large predators, like brown bear (*Ursus arctos*) and wolf (*Canis lupus*), are almost absent in the study area (Svensson et al. 2017, Fløystad et al. 2018).

2.2 Moose hunting units

All moose hunting units within the two municipalities were included in the study (Fig. 1 b). Moose hunting units are the smallest administrative unit for moose management and typically includes the land of several land owners. Most hunting units cover a forested area of about 10-100 km². The hunting units were used as the spatial unit in the analyses. Maps showing borders of the the hunting units were obtained from the municipality wildlife management authorities and leaders of each hunting unit. There were in total 74 active hunting units in Stjørdal and Meråker, and even though the borders may have shifted somewhat during the study period, the changes were minor and not expected to affect the habitat configuration of the unit. Accordingly, the most recent map, from 2017, provides a reasonable precise depiction of the hunting units during the study period (2006-2016).

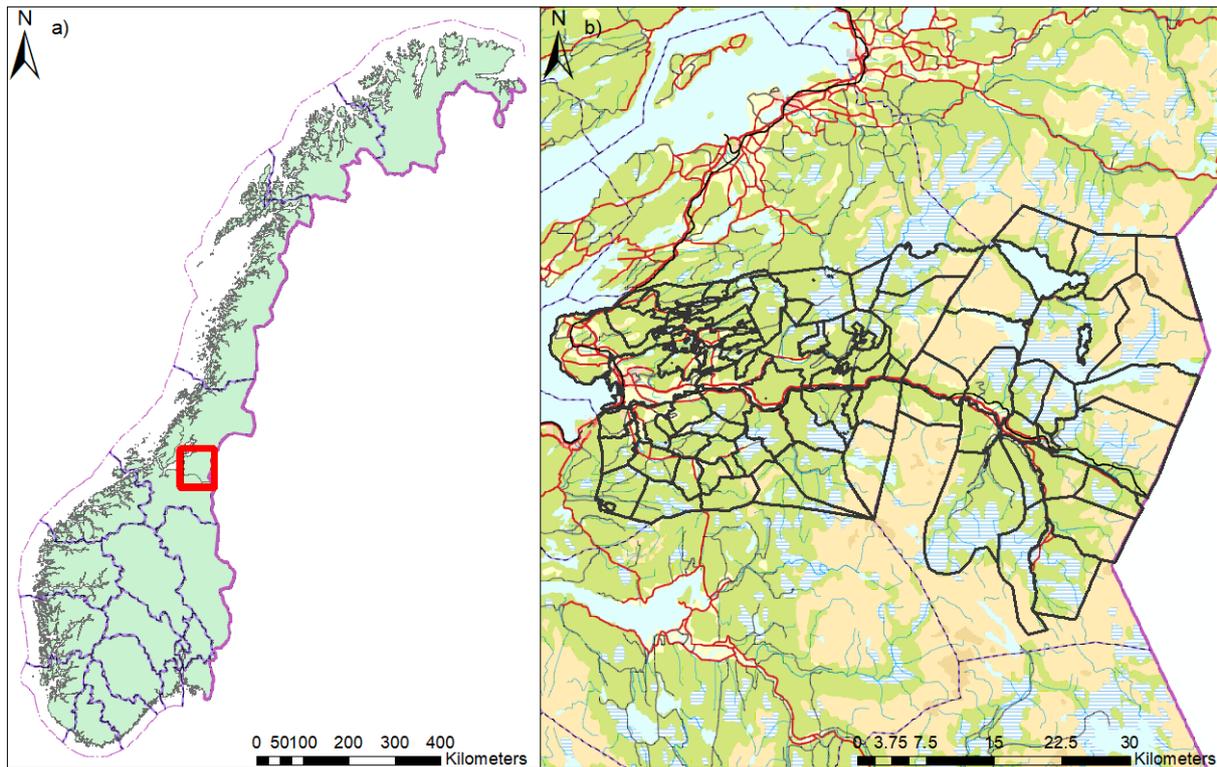


Fig. 1: a) The location of the study area (red square), and b) the location of the 74 hunting units marked with solid dark grey lines from which the moose data originates.

2.3 Moose life history data

As a measure of early-life body mass, I used the carcass mass of harvested calves and yearlings. These are collected as a part of the National monitoring program for cervids in Norway, that is operated by the Norwegian Institute for Nature Research (NINA) (Solberg et al. 2017). The carcass mass is the weight of the moose after head, skin, viscera, lower legs and bleedable blood have been removed, and constitutes normally of 50-56% of the live weight (Solberg et al. 2008, Garel et al. 2009). The carcass mass is measured by the hunters within each hunting unit. In addition, the hunters register to kill date, location, sex and age class (calf, yearling, adult) of the moose. Calves and yearlings are aged by the tooth replacement patterns by the hunters, but when in doubt, hunters send yearling jaws together with all adult jaws to the laboratory at NINA for accurate age determination based on counting of annuli in the cementum of the incisor (Rolandsen et al. 2008).

During the study period, 2006-2016, the moose hunting mainly occurred in September and October, except for the last few years when the hunting season was extended to also include November and December. However, to reduce the variation in body mass due to late kill date, I only used body mass data from individuals killed within the original hunting period (25th of September - 31st of October). In total, I used data from 2571 calves, 398 female

yearlings and 746 male yearlings. The carcass masses were adjusted for kill date to the first day of hunting, the 25th of September, using separate regressions for calves and yearlings. Calves (female and male combined) were found to gain 0.156 kg pr. day ($\beta = 0.156 \pm 0.02$, $p < 0.001$) and male calves were on average 3.719 kg ($\beta = 3.719 \pm 0.44$, $p < 0.001$) heavier than female calves. Female yearlings gained 0.098 kg pr. day ($\beta = 0.098 \pm 0.08$, $p = 0.243$), whereas male yearlings lost 0.124 kg pr. day ($\beta = -0.124 \pm 0.06$, $p = 0.049$). Male yearlings were on average 9.640 kg ($\beta = 9.640 \pm 0.16$, $p < 0.001$) heavier than female yearlings.

I used moose hunter observations to estimate the twinning rate within hunting units. These data are collected and reported by the hunting teams within each hunting unit and comprise all moose seen per hunting season (Solberg et al. 2006). The moose observations are classified according to six categories: calves, adult females without calf, adult females with one calf, adult females with two calves, adult males and adult moose of unknown sex and/or age (Solberg and Sæther 1999). Twinning rate is often used as an index of population productivity and is calculated as the proportion twin producing females (seen females with two calves) of all calf-producing females (females observed with one or two calves) (Solberg et al. 2006).

2.4 Habitat characteristics of the hunting units

I used two different thematic maps to describe the habitat types within the study area: 1) Area resource maps 1:50 000 (AR50), which covers the entire land surface, and 2) Forestry maps (SatSkog) which have information on tree species, stand age and forest productivity class. SatSkog only covers the forested areas. Both AR50 and SatSkog maps are provided by the Norwegian Institute of Bioeconomy Research (NIBIO, www.nibio.no). Based on area types from AR50, I classified the hunting units to agricultural areas, barren land and bog, and forest (Table 1), while SatSkog was used to classify the forest into deciduous and mixed forest, mixed coniferous and pine forest and spruce dominated forest. As a measure of site productivity, I used the forest productivity classes from AR50. The categories impediment and low productivity class were pooled to one class, and likewise I pooled intermediate and high productivity class (Table 1). Elevation (m. asl.) was obtained from a digital elevation model with resolution 25x25m² from the Norwegian Mapping Authority (www.kartverket.no). For description of the habitat types used to characterise the hunting units, see Table 1.

Table 1: Source and description of the habitat characteristics used to explain the spatial variation in carcass masses and twinning rate. Total range (min, max) and mean for each habitat characteristic within the hunting units are included.

Source	Habitat characteristic	Description	Range: Min; mean; max
AR50 Area type	Agricultural areas	Areas used for agricultural purposes, i.e. tilled farmland, surface cultivated farmland and non-tilled farmlands used for livestock grazing	0.00; 0.10; 0.49
	Forest	Forest covered land, i.e., forested areas which are not barren bog	0.11; 0.61; 0.87
	Barren land and bog	Solid ground consisting of vegetation which is not forest, combined with areas with the surface consisting of bog	0.02; 0.28; 0.88
SatSkog Dominating tree species	Deciduous and mixed forest	Dominating tree species being deciduous, combined with areas dominated by mixed tree species	0.00; 0.07; 0.17
	Mixed coniferous and pine forest	Dominating tree species being coniferous combined with areas dominated by pine forest	0.01; 0.12; 0.30
	Spruce dominated forest	Spruce as dominating tree species	0.01; 0.40; 0.75
AR50 Forest productivity class	Impediment and low productivity class	Areas categorized as impediment and low ability to produce timber	0.02; 0.39; 0.87
	Intermediate and high productivity class	Areas categorized as intermediate, high and particularly high ability to produce timber	0.00; 0.36; 0.71
DEM	Elevation	Mean elevation of hunting units as calculated from a digital elevation model (m. asl.)	63.95; 331.31; 707.32

For each hunting unit, I calculated the proportion of the different habitat types relative to the area that is considered relevant for the moose (i.e. excluding lakes, densely populated areas and areas not mapped due to high alpine areas), as well as the mean elevation of each hunting unit. The habitat distribution in the study area is indicated in Fig.2.

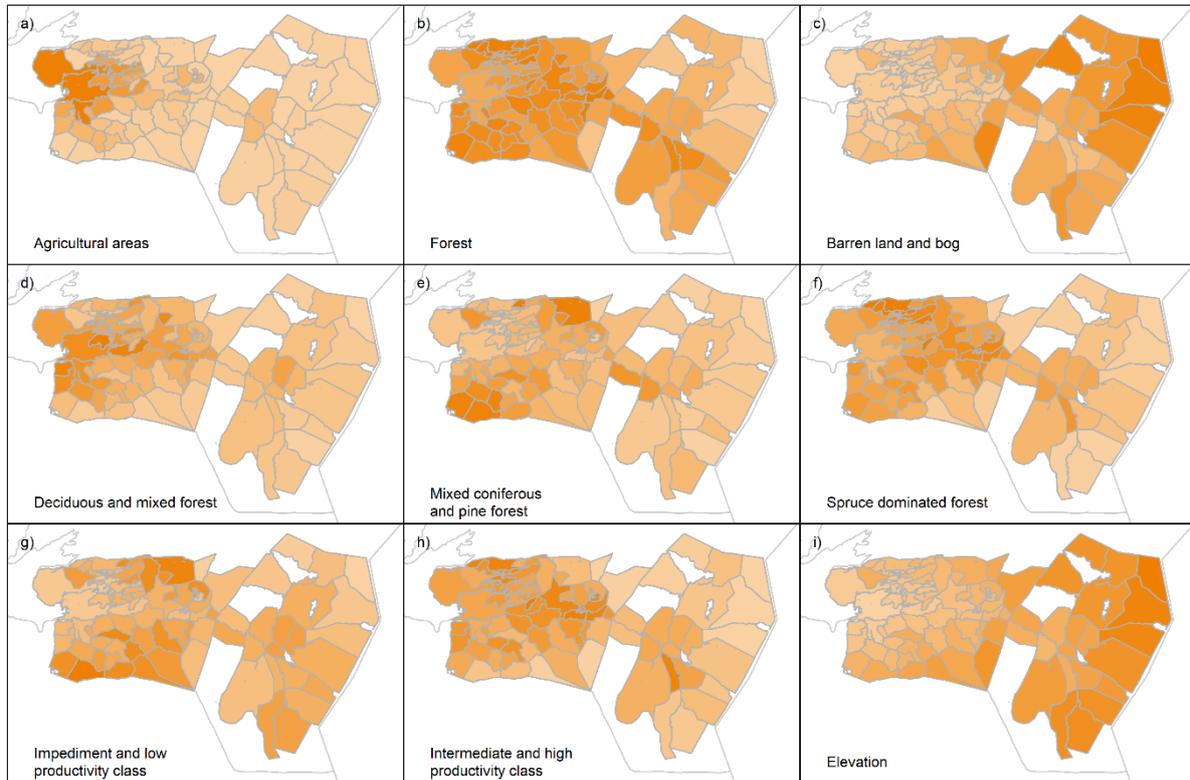


Fig. 2: Spatial patterns of proportion land cover and elevation of each habitat type in the different hunting units. More intense colour indicates higher proportion land cover and elevation.

2.5 Statistical analyses

First, I investigated the spatial variation in life history traits among hunting units, and explored the covariation between the moose life history traits. These analyses were done by using the mean for each life history trait within each hunting unit.

Secondly, I ran univariate tests to assess which of the explanatory variables related to the habitat characteristics, that best explained the variation in calf, female yearling, and male yearling carcass mass, as well as twinning rate among hunting units. For carcass mass, I fitted linear mixed-effect models (LMM) using the lmer-function from lme4-package (Bates et al. 2014), because data are structured on individual level and therefore is exposed to both spatial (individuals killed within the same hunting unit) and temporal (individuals killed within the same year) autocorrelation (Bolker et al. 2009). Thus, hunting unit and year were included as

random factors. For calf carcass mass, twinning rate was included as explanatory variable in addition to the habitat characteristics, to check whether high twinning rate affects calf carcass mass (i.e., a trade-off between offspring quantity and quality). For twinning rate, I fitted univariate generalized linear mixed-effect models (GLMM) using the `glmer`-function from the `lme4` package (Bates et al. 2014). GLMM allows for a binomial response in the models, and twinning rate can be expressed as a logistic regression with the number of adult females with twins as success and adult females with one calf as failure. The data on twinning rate was aggregated within year for each hunting unit, and I accounted for the spatial autocorrelation by defining hunting unit as random factor (Bolker et al. 2009). In addition to the habitat characteristics, female yearling carcass mass was included as an explanatory variable for twinning rate, to investigate whether large female yearling carcass mass may indicate the presence of large adult females, and hence higher production of twins. For all statistical tests, I also calculated the marginal R^2 (R^2_m) following Nakagawa and Schielzeth (2013).

Finally, I used the explanatory variables from the univariate tests with a p-value <0.100 , in multivariate analyses to determine the most influential explanatory variable(s) for each life history trait. The model selection was based on the Akaike information criterion, corrected for small sample sizes (AIC_c , Burnham and Anderson 2002), and conducted by using the `dredge`-function from the `MuMIn`-package (Barton and Barton 2018). The models with the lowest AIC_c were considered most parsimonious and that ‘best’ model applied to the data among the candidate models (Burnham and Anderson 2002). Models were fitted with maximum likelihood (ML) for calculating the AIC_c -values, whereas parameter estimates and all univariate models were fitted with restricted maximum likelihood (REML).

Most habitat characteristics had a left-skewed distribution, and such non-normal distributions may affect the results. To investigate whether this was the case in my analyses, I re-ran all analyses with square-root transformed explanatory variables (Crawley 2013). The main results remained similar, and I therefore choose to present results based on untransformed variables to ease the interpretation. See tables A.1-A.3 for the results based on analyses using transformed variables. All analyses were conducted using R Statistical software version 3.4.2 (R Core Team 2018).

3. Results

3.1 Spatial patterns and covariation in life history traits

There was large variation in the mean carcass mass and twinning rate among hunting units. Mean calf carcass mass ranged from 47 kg to 67 kg (mean = 57 kg, SD = 5, N = 73), female yearling carcass mass ranged from 99 to 150 kg (mean = 119 kg, SD = 11, N = 67), yearling male carcass mass ranged from 99 to 138 kg (mean = 119 kg, SD = 9, N = 73) and twinning rate ranged from 0.02 to 0.52 twin producing females of all calf producing females (mean = 0.21, SD = 0.12, N = 67).

There were quite clear spatial patterns in the life history traits among hunting units. Male yearling carcass masses and twinning rate were higher in the western hunting units close to the fiord, whereas the calf carcass masses appeared to be higher in the eastern hunting units at high elevation. Female yearling carcass masses varied throughout the study area, and seemed especially large in few hunting units (Fig. 3; Table A.4).

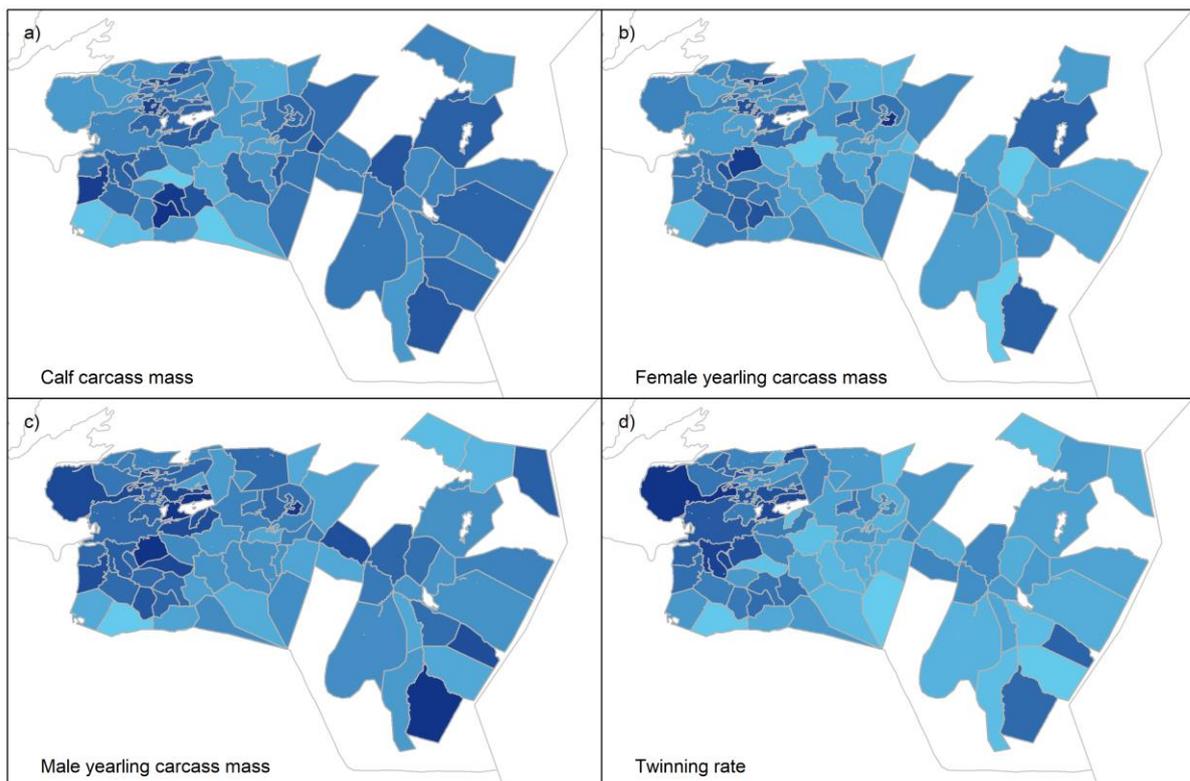


Fig. 3: Spatial patterns for the mean of the life history traits pr. hunting unit for a) calf carcass mass, b) female yearling carcass mass, c) male yearling carcass mass, d) and twinning rate. More intense colour indicates higher carcass masses a-c) and twinning rate d). Some hunting units are missing colouration due to no data for the specific life history trait (Table A.4).

There was positive covariation between life history traits (Fig. 4). Linear regression performed on the mean of each life history trait per hunting unit showed that calf carcass mass covaried significantly with female yearling carcass mass (1.185 ± 0.263 SE, $p < 0.001$, $r^2 = 0.22$, Fig. 4 a), male yearling carcass mass (0.890 ± 0.221 SE, $p < 0.001$, $r^2 = 0.17$, Fig. 4 b), and twinning rate (0.009 ± 0.003 SE, $p = 0.003$, $r^2 = 0.10$, Fig. 4 c). Female yearling carcass mass showed significant covariation with twinning rate (0.005 ± 0.001 SE, $p < 0.001$, $r^2 = 0.26$, Fig. 4 d), and a similar result was found between male yearling carcass mass and twinning rate (0.007 ± 0.001 SE, $p < 0.001$, $r^2 = 0.30$, Fig. 4 e).

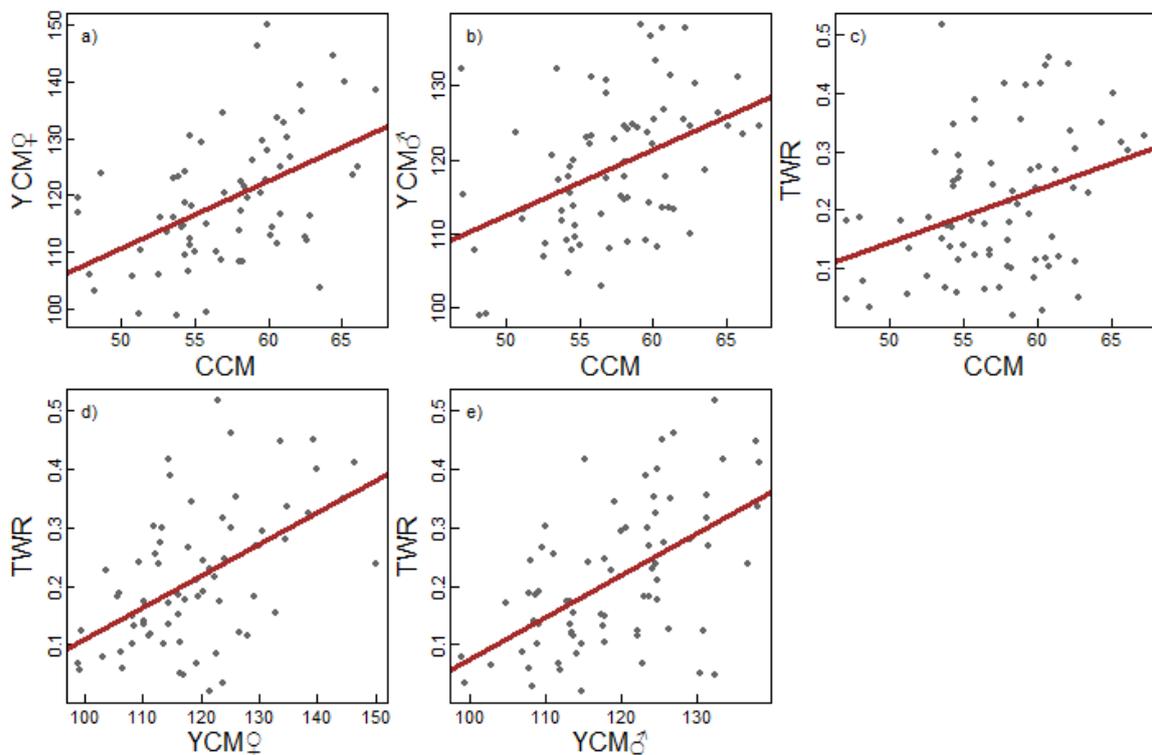


Figure 4. Covariation between life history traits: calf carcass mass (CCM), female yearling carcass mass (YCM ♀), male yearling carcass mass (YCM ♂) and twinning rate (TWR). Linear regression on the mean for each life history trait per hunting unit was used to assess the covariation.

3.2 Habitat and calf carcass mass

The univariate tests for calf carcass mass showed significant positive relationships with agricultural areas and significant negative relationship with mixed coniferous and pine forest, and with impediment and low productivity class (Table 2). The remaining habitat characteristics and twinning rate were not significantly related to calf carcass mass (Table 2; Fig. A.1). However, deciduous and mixed forest, as well as twinning rate had p -values < 0.100 (Table 2), and were included in the multivariate modelling.

Table 2: Parameter estimates (\pm standard error) for life history traits (LHT) for calf carcass mass (CCM), yearling female carcass mass (YCM ♀) and male yearling carcass mass (YCM ♂) from univariate lmer-models controlling the effect of hunting unit and year, and twinning rate (TWR) from univariate glmer-models controlling for the effect of hunting unit. T/z-values are included in addition to p-values and R²m. Statistical significant ($p < 0.050$) effects are marked bold, whereas variables with strong support ($p < 0.100$) that were included in the multivariate models are marked by italic font. Parameter estimates for twinning rate are at the logit-scale. $N_{\text{calves}} = 2571$, $N_{\text{yearling♀}} = 398$, $N_{\text{yearling♂}} = 746$, $N_{\text{hunting unit}} = 74$, $N_{\text{year}} = 11$.

Explanatory variable	LHT	$\beta \pm \text{SE}$	t/z-value	p-value	R ² m
Agricultural areas	CCM	10.120 \pm 0.951	2.70	0.009	0.017
	YCM ♀	27.141 \pm 8.341	3.25	0.002	0.056
	YCM ♂	32.799 \pm 5.738	5.72	<0.001	0.073
	TWR	3.567 \pm 0.467	7.64	<0.001	0.061
Forest	CCM	-1.595 \pm 3.090	-0.52	0.607	<0.001
	YCM ♀	1.280 \pm 8.160	0.16	0.876	<0.001
	YCM ♂	-1.633 \pm 5.750	-0.28	0.777	<0.001
	TWR	0.286 \pm 0.542	0.53	0.597	<0.001
Barren land and bog	CCM	-3.082 \pm 2.483	-1.24	0.218	0.003
	YCM ♀	-16.015 \pm 6.365	-2.52	0.014	0.025
	YCM ♂	-12.765 \pm 4.380	-2.91	0.004	0.020
	TWR	-1.821 \pm 0.394	-4.63	<0.001	0.040
Deciduous and mixed forest	CCM	20.975 \pm 12.226	1.72	0.091	0.006
	YCM ♀	49.250 \pm 29.751	1.66	0.103	0.013
	YCM ♂	73.171 \pm 21.264	3.44	0.001	0.032
	TWR	8.340 \pm 1.953	4.27	<0.001	0.032
Mixed coniferous and pine forest	CCM	-15.626 \pm 6.864	-2.28	0.026	0.009
	YCM ♀	10.625 \pm 17.457	0.61	0.545	0.002
	YCM ♂	-6.973 \pm 13.802	-0.51	0.615	<0.001
	TWR	0.881 \pm 1.233	0.72	0.475	0.001
Spruce dominated forest	CCM	1.207 \pm 2.695	0.45	0.656	<0.001
	YCM ♀	3.283 \pm 7.096	0.46	0.645	<0.001
	YCM ♂	4.952 \pm 5.074	0.98	0.332	0.003
	TWR	0.813 \pm 0.474	1.71	0.087	0.006
Impediment and low productivity class	CCM	-8.416 \pm 2.633	-3.20	0.002	0.017
	YCM ♀	-7.847 \pm 6.903	-1.14	0.260	0.006
	YCM ♂	-11.390 \pm 5.087	-2.24	0.028	0.014
	TWR	-0.987 \pm 0.463	-2.13	0.033	0.010
Intermediate and high productivity classes	CCM	3.884 \pm 2.839	1.37	0.175	0.004
	YCM ♀	4.371 \pm 7.494	0.58	0.561	0.001
	YCM ♂	8.072 \pm 5.353	1.51	0.136	0.006
	TWR	0.886 \pm 0.496	1.79	0.074	0.007
Elevation	CCM	-0.004 \pm 0.004	-1.11	0.272	0.003
	YCM ♀	-0.020 \pm 0.009	-2.28	0.026	0.023
	YCM ♂	-0.020 \pm 0.006	-3.36	0.001	0.027
	TWR	-0.003 \pm 0.001	-5.41	<0.001	0.048
TWR	CCM	2.374 \pm 1.366	1.74	0.082	0.002
YCM ♀	TWR	0.033 \pm 0.007	4.72	<0.001	0.037

Table 3: AIC_c- based ranking of models explaining the spatial variation for the life history traits (LHT): calf carcass mass (CCM), female yearling carcass mass (YCM ♀), male yearling carcass mass (YCM ♂) and twinning rate (TWR) using multivariate lmer-models for carcass mass, controlling for the effect of hunting unit and year, and multivariate glmer-models for TWR controlling for the effect of hunting unit, with the significant variables found in Table 1. Variables included in the global model for each LHT are shaded grey and the variables included in the candidate model are indicated by an x. ΔAIC_c indicate the difference between the best model (model 1) and the candidate models. Only the models with ΔAIC_c < 2 are presented.

Model	LHT	Agricultural areas	Barren land and bog	Deciduous and mixed forest	Mixed coniferous and pine forest	Spruce dominated forest	Impediment and low productivity class	Intermediate and high productivity class	Elevation	TWR	YCM ♀	K	ΔAIC _c	AIC _c weight	R ² m
1	CCM						x			x		6	0.00	0.111	0.019
2	CCM						x					5	0.35	0.093	0.017
3	CCM	x					x					6	0.83	0.073	0.023
4	CCM	x					x			x		7	1.16	0.062	0.024
5	CCM			x			x					6	1.31	0.058	0.020
6	CCM			x			x			x		7	1.32	0.058	0.022
7	CCM	x			x							6	1.52	0.052	0.023
8	CCM	x			x					x		7	1.86	0.044	0.024
9	CCM				x		x			x		7	1.92	0.042	0.019
1	YCM ♀	x										5	0.00	0.404	0.055
2	YCM ♀	x	x									6	1.48	0.193	0.055
1	YCM ♂	x										5	0.00	0.251	0.073
2	YCM ♂	x					x					6	1.67	0.109	0.074
3	YCM ♂	x		x								6	1.74	0.105	0.073
4	YCM ♂	x							x			6	1.95	0.095	0.074
1	TWR	x		x		x		x			x	7	0.00	0.077	0.080
2	TWR	x				x		x			x	6	0.17	0.071	0.079
3	TWR	x					x				x	5	0.82	0.051	0.078
4	TWR	x				x	x	x			x	7	0.88	0.050	0.081
5	TWR	x				x	x				x	6	1.29	0.041	0.082
6	TWR	x		x		x	x	x			x	8	1.31	0.040	0.082
7	TWR	x		x			x				x	6	1.87	0.030	0.080
8	TWR	x	x	x		x		x			x	8	1.96	0.029	0.081
9	TWR	x	x			x		x			x	7	1.99	0.029	0.079

The global multivariate model included agricultural areas, deciduous and mixed forest, mixed coniferous and pine forest, impediment and low productivity class, and twinning rate (Table 3). According to the AIC_c-value, the most parsimonious multivariate model for calf carcass mass included impediment and low productivity class, and twinning rate (Table 3).

However, an alternative candidate model that also received support ($\Delta AIC_c = 0.35$), only included impediment and low productivity areas (Table 3). Due to large standard error for the effect of twinning rate in the most parsimonious model (2.083 ± 1.366 , $p=0.128$), the model ranked second best in Table 3 was chosen for presentation. Calf carcass mass was negatively related to the proportion of impediment and low productivity class in the hunting unit (Table 4; Fig. 5)

Table 4: Parameter estimates ($\beta \pm SE$) from the model ranked number two in the multivariate lmer analyses based on AIC_c -values explaining the spatial variation in calf carcass mass. The model controls for the effect of hunting unit and year. $N_{calves} = 2571$, $N_{hunting\ unit} = 74$, $N_{year} = 11$.

	$\beta \pm SE$	t-value	p-value
Intercept	60.766 ± 1.317	46.13	<0.001
Impediment and low productivity class	-8.408 ± 2.611	-3.22	0.002

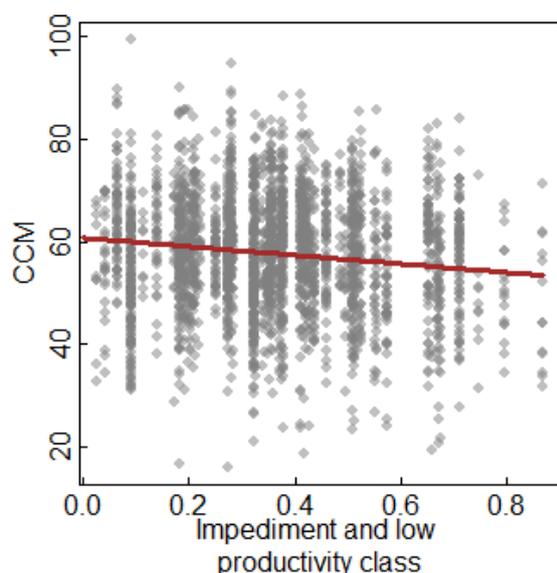


Fig. 5: The relationship between calf carcass mass (CCM) and the proportion of impediment and low productivity class in the hunting units within Stjørdal and Meråker municipalities.

3.3 Habitat and yearling carcass mass

The univariate tests revealed a significant positive relationship between yearling carcass mass (both sexes) and agricultural areas, and a significant negative relationship with barren land and bog, and elevation (Table 2). Male yearling carcass mass showed also a significantly positive relationship with deciduous and mixed forest, and a significant negative relationship

with impediment and low productivity class (Table 2). The remaining explanatory variables were not significantly related to yearling carcass mass (all p-values > 0.103, Table 2; Fig. A.2-A.3).

The most parsimonious models for yearling carcass mass (both sexes) included only the proportion of agricultural areas (Tables 3), and, alternative candidate models had relatively low support ($\Delta AIC_c > 1.48$). For both males and females, the relationship between carcass mass and proportion of agricultural areas was positive (Table 5; Fig. 6)

Table 5: Parameter estimates ($\beta \pm SE$) from the models ranked as best in the multivariate lmer analyses based on AIC_c -values explaining the spatial variation in female yearling carcass mass ($YCM_{\text{♀}}$) and male yearling carcass mass ($YCM_{\text{♂}}$), while controlling for the effect of hunting unit and year. $N_{YCM_{\text{♀}}} = 398$, $N_{YCM_{\text{♂}}} = 746$, $N_{\text{hunting unit}} = 74$, $N_{\text{year}} = 11$.

	$\beta \pm SE$	t-value	p-value
$YCM_{\text{♀}}$			
Intercept	116.164 \pm 1.917	60.58	<0.001
Agricultural areas	27.141 \pm 8.341	3.254	0.002
$YCM_{\text{♂}}$			
Intercept	115.369 \pm 1.407	82.00	<0.001
Agricultural areas	32.799 \pm 5.738	5.72	<0.001

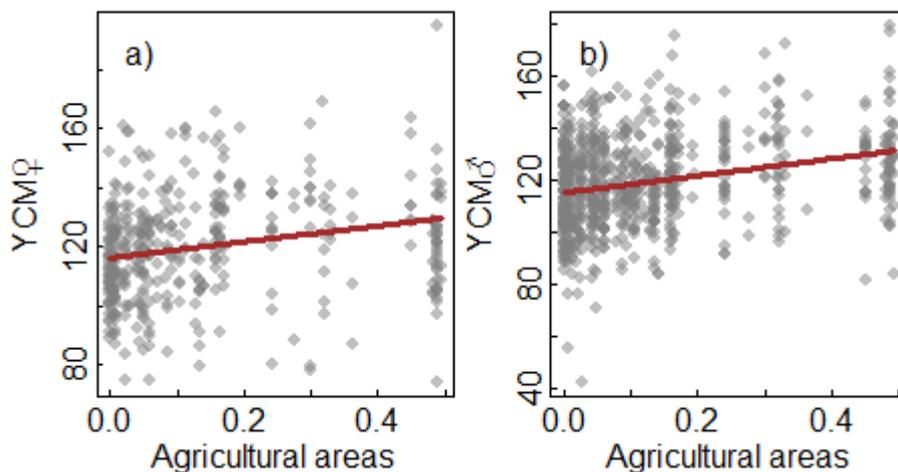


Fig. 6. The relationship carcass mass and the proportion of agricultural areas in the hunting units for a) female ($YCM_{\text{♀}}$), and b) male yearling moose ($YCM_{\text{♂}}$) in Stjørðal and Meråker municipalities.

3.4 Habitat and twinning rate

The univariate tests for twinning rate showed significant positive relationships with agricultural areas, deciduous and mixed forest and female yearling carcass mass, and significant negative relationships with barren land and bog, impediment and low productivity class and elevation (Table 2). The remaining habitat characteristics had non-significant

relationships with twinning rate (Table 2; Fig. A.4). However, the following variables had p-values < 0.100 , and were included in the multivariate modelling: spruce dominated forest, and intermediate and high productivity classes (Table 2).

The global multivariate model explaining twinning rate included agricultural areas, barren land and bog, deciduous and mixed forest, spruce dominated forest, impediment and low productivity class, intermediate and high productivity classes, elevation and female yearling carcass mass (Table 3). The most parsimonious model for twinning rate included agricultural areas, deciduous and mixed forest, spruce dominated forest, intermediate and high productivity classes and female yearling carcass mass. However, an alternative model without deciduous and mixed forest had a ΔAIC_c of only 0.17 (Table 3). Moreover, the parameter estimate of deciduous and mixed forest had quite high uncertainty ($\beta = 2.949 \pm 1.967$ SE, $p = 0.134$), and I therefore choose to present the model ranked as second best. According to this model, there were positive relationships between twinning rate and the proportion of agricultural areas, spruce dominated forest, and yearling female carcass mass, whereas twinning rate was negatively related to the proportion of intermediate and high productivity class (Table 6; Fig. 7)

Table 6: Parameter estimates ($\beta \pm SE$) from the model ranked number 2 in multivariate glmer analyses based on AIC_c values explaining the spatial variation in twinning rate. The model controls for the effect of hunting unit. All estimates are at logit-scale. $N_{\text{hunting unit}}=74$, $N_{\text{year}}=11$.

	$\beta \pm SE$	z-value	p-value
Intercept	-3.645 ± 0.652	-5.59	<0.001
Agricultural areas	3.440 ± 0.477	7.21	<0.001
Spruce dominated forest	1.721 ± 0.644	2.67	0.008
Intermediate and high productivity class	-1.684 ± 0.694	-2.43	0.015
YCM ♀	0.016 ± 0.006	2.82	0.005

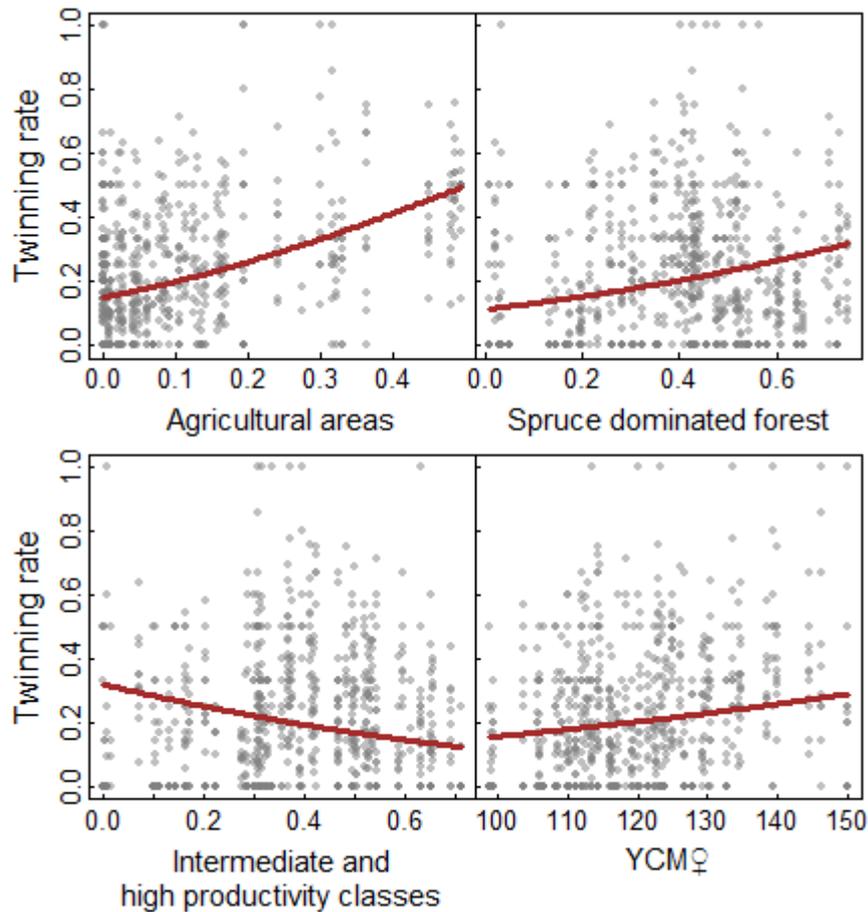


Fig. 7. The relationships between twinning rate (TWR) and the proportion of agricultural areas, deciduous and mixed forest, spruce dominated forest, intermediate and high productivity classes, and the carcass mass of females ($YCM_{\text{♀}}$) in the hunting units in Stjørdal and Meråker municipalities.

4. Discussion

My results show that there exists small-scale geographic variation in both carcass mass and twinning rate of moose, and a rather high positive covariation between the life history traits (Figs. 3 - 4). Moreover, the observed small-scale spatial patterns in life history traits could be explained by variation in habitat composition within the hunting units, where some habitat characteristics showed repeated significant occurrences for life history traits (Table 3). The proportion of agricultural areas seemed to be the most important variable, as it was positively related to both yearling carcass mass and twinning rate. Whereas the proportion impediment and low productivity class, and barren land and bog, were found to have the overall most negative influence on the life history traits (Table 3). However, for calf body mass, agricultural areas, which had high explanatory power for yearling carcass mass and twinning rate, did not turn out as an important variable (Table 3). Moreover, there was not statistical

support that twinning rate explained the variation in calf carcass mass. This indicates that high-quality areas do not have calves that are particularly larger, or smaller, than the average, but instead adult females produce two intermediate-sized offspring rather than one large calf in such areas. Yearling carcass mass and twinning rate showed substantial covariation and mainly the same habitat characteristics were associated with these life history traits (Table 3). In addition to several habitat characteristics, twinning rate showed a significant positive relationship with female yearling carcass mass (Table 6), which confirms the positive relationships between body mass and fecundity in moose, e.g. Markussen et al. (2018).

Environmental conditions during summer have previously been shown most important for body growth and development in temperate ungulates (White 1983, Hjeljord et al. 1990, Herfindal et al. 2006b). During summer, the quantity and accessibility of forage is normally not limiting, however, the quality of forage may vary much, and is accordingly found important for moose life history traits such as body mass. Previous studies on moose habitat utilisation suggest that agricultural areas are important during summer (Herfindal et al. 2009, Bjørneraas et al. 2011, Bjørneraas et al. 2012), and in line with these studies, I found that both yearling carcass mass and twinning rate were positively related to the proportion of agricultural areas within the hunting units (Tables 3). However, agricultural areas are correlated with several other habitat characteristics (Table A.5), and especially positively correlated with deciduous and mixed forest, which also have been found to be preferred by moose for both foraging and cover-availability (Bjørneraas et al. 2011).

There may be several reasons to why agricultural areas are of such large importance for moose life history traits. The soil tilling starts as early as possible to optimise the forage production, which may provide moose with early access to high-quality forage. In forested areas, however, the snow cover is staying longer and the green-up starts later. Because multicultural grass-production usually have several harvests during the growing season, the same fields may also flourish with early-stage, highly nutritional plants several times per summer. Plants at such early phenological stage have higher nutrient content and a higher digestibility than more mature plants (Deinum 1984), with positive consequences of large herbivores (Langvatn and Albon 1986, Langvatn et al. 1996). Moreover, the abundance and density of forage is high in agricultural areas, which increase the efficiency with which moose can consume agricultural plants such as grasses. In addition, the small-scale habitat fragmentation of agricultural landscapes provides at the same time access to high quality forage and cover in nearby forest patches, and thus contain several important habitat-features within short distance. Access to heterogeneous landscapes has been shown to be important for

ungulates to fulfil their physiological demands (Van der Wal et al. 2000, Hawkins et al. 2003, Bjørneraas et al. 2012).

It is expected that single calves are heavier than twin calves, due to resource allocation between two offspring instead of one (Sæther et al. 1996). I did not find significant support for that calf carcass mass was related to twinning rate, which may suggest that any trade-off between offspring quantity and quality is weak in my study area. However, one factor may affect the ability to detect such a trade-off is that calf body mass was measured as carcass mass during autumn, 3-4 months after birth. Accordingly, a higher growth rate in high-quality areas with a high twinning rate may allow calves to compensate for a lower birth weight, and even become larger than singletons in low-quality areas at the time of the autumn hunt. This will cause a weaker trade-off signal during autumn compared to the time at birth.

Disentangling these mechanisms was unfortunately not able with the data I had available.

Interestingly, the R^2 -values from the multivariate tests revealed large variation in how strong the life history traits were related to the habitat variables (Table 3). The R^2 -values for female yearling carcass mass, male yearling carcass mass and twinning rate was found to be two to threefold as large as the values for calf carcass mass (Table 3). This is another indication that calf carcass mass is influenced by other mechanisms than directly by habitat quality. This can for instance be the age of female segment in the area, as maternal age has been shown to be important for the size of the calf (Solberg et al. 2007). However, as also twinning rate is related to maternal age (Markussen et al. 2018), and I would have expected a closer relationship between mean calf carcass mass and twinning rate. Alternatively, the relationship between habitat and autumn carcass mass of calves is weakened by the fact that carcass mass is affected by a calf being twin or singleton. This would affect both birth mass and maternal resource allocation per offspring during lactation period, which could reduce the habitat signal through high-producing females allocate less resources per offspring. The result would be that the trade-off a female make between number and quality of offspring is compensated for already during the first summer.

Twinning rate is often used as a population productivity index (Solberg et al. 2006), and may be influenced by individual differences in e.g., body size (Markussen et al. 2018), through environmental variation (Sæther 1985), variation in forage quality and availability (White 1983) and environmental stress (e.g., population density Pettorelli et al. 2001). The results show that the mean twinning rate in the study area is somewhat lower (0.21, SD = 0.12, N = 67), compared to a study which assessed a large part of Norway, which found a higher twinning rate (0.28, SD = 0.14, N = 936, Tiilikainen et al. 2012). This indicates that the

moose population in the study area is not among the high-performing in Norway. This study does not consider the population density in the study area, however, the National monitoring program for cervids in Norway have found that the population density has been high and increased until 2004 and more or less stable since then (Solberg et al. 2017). The high-quality areas are likely to hold the highest number of individuals, and the influence of the habitat types may be under estimated in this study, due to density-dependent factors. Unfortunately, population density estimates are not available on such a small-scale and have therefore not been tested. High population density and/or resource depletion can have density dependent ramifications, which first is visualised as reduced juveniles body mass, whereas a decrease in female fecundity is expected to occur somewhat later (Mysterud 2006).

The multivariate tests showed the most parsimonious model for twinning rate included agricultural areas, deciduous and mixed forest, spruce dominated forest, intermediate and high productivity classes and female yearling carcass mass (Table 3). However, the large uncertainty for the effect of deciduous and mixed forest raise doubt for the importance for this variable. Deciduous and mixed forest might be important for twin-producing females during winter, due to winter browse (Rolandsen et al. 2010, Wam and Hjeljord 2010a). Similarly, spruce dominated forests which is subject to intensified forestry has a high proportion of the areas in young age-classes with high availability of deciduous species (Bjørneraas et al. 2012), which can explain its significant relationship with twinning rate (Table 6). The effect of intermediate and high productivity classes altered from being positively related in univariate tests (Table 2), to become negatively related to twinning rate is the most parsimonious model in multivariate tests (Table 6), when accounted for the effect of the other explanatory variables. This can be explained by the high correlation between agricultural areas and intermediate and high productivity class (Table A.5).

In ungulates, the general patterns is a positive relationship between adult body mass and female fecundity (Gaillard et al. 2000a), and this is also found in moose (Sæther and Haagenrud 1985b, Markussen et al. 2018). In line with this, I found positive relationships between twinning rate and yearling carcass mass. Although yearlings not yet have reproduced, their body mass is a good indicator for adult body mass (Garel et al. 2006), and areas with large female yearlings can therefore be expected to also have large adult females. Interestingly, the effect size of female yearling carcass mass related to twinning rate was reduced when correcting for the effect when correcting for the effect of the habitat characteristics (Tables 2; 6). This strengthens the evidence that habitat drives the spatial variation in fecundity in moose.

The extent of the study area is small compared to the distances the moose are known to be able to travel within a season (Rolandsen et al. 2010), suggesting that individuals can move from low-quality areas to high-quality areas in the study area within just a few days. Several of the hunting units are also smaller than the estimated summer home range size (Rolandsen et al. 2010). It may therefore be possible for individuals in poor-quality areas to move and settle in high-quality areas. However, the presence of clear spatial patterns in life history traits, and the strong explanatory power of habitat characteristics, suggest that this is not the case in the study area. Most likely, individuals stay and settle in proximity to its natal areas. Young moose usually migrate from natal areas when 1-3 years old (Rolandsen et al. 2010). Accordingly, the dispersal phase may not be finished for yearlings, and mixing of individuals between areas may occur at older age. Still, the strong geographical structure of twinning rate that confirms patterns of body mass variation of yearlings suggest that long-distance dispersal is not important for shaping geographical variation in life history traits in this population. Alternatively, high-quality females are found in areas which provide good foraging condition and hence produce many intermediate-sized calves, which in turn experience good living conditions in their first year of life.

Whereas many studies show large-scale variation in life history traits in relation to habitat and environmental conditions, I have documented that such variation exists even at small spatial scales within the distance of individual can move in a few days. Accordingly, the role the landscape has in shaping life history variation and population dynamics must be understood at the within-population level, not assuming that individuals are distributed according to availability of resources, e.g., Fretwell and Lucas (1969). My results emphasize the importance of small-scale geographical variation in habitat composition for fitness-related traits. However, it also shows that trade-offs between life history traits such as offspring size and quantity, may weaken the habitat-signal.

Acknowledgements

First, I would like to thank the Norwegian Institute for Nature Research (NINA) for access to quality-ensured hunting data on moose and for estate files enabling the digitizing of the map over hunting units in Stjørdal and Meråker, and the Norwegian University of Science and Technology (NTNU) for the opportunity of doing my thesis.

I am also sincerely grateful for my excellent supervisors; Ivar Herfindal, Erling J. Solberg, Vidar Grøtan and Christer M. Rolandsen for their assistance, advice throughout this project and interesting discussions. I would also like to thank the wildlife management authorities in Stjørdal and Meråker, and the leaders of the hunting units for their collaboration enabling me to digitize the map over the hunting units; Stian Almestad, John Morten Husbyn, John Ole Bakheim, Magnar Bremseth and Anne Haneborg. I would also like to thank my fellow students, especially Ida, Veronica, Live, Ingegjerd and Kristina for their support, science-related discussions and for making the years at NTNU so great.

Last, but not least, I am forever grateful to my parents for their encouragement, support and tolerance for all my, sometimes ‘over-the-top’ creative, ideas and decisions, and for teaching me to appreciate, explore and love the wonders of nature. I would also like to thank my boyfriend for his support, patience and devotion.

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6. Appendix

Table A.1: Parameter estimates (\pm standard error) for life history traits (LHT) for calf carcass mass (CCM), yearling female carcass mass (YCM ♀) and male yearling carcass mass (YCM ♂) from univariate lmer-models controlling the effect of hunting unit and year, and twinning rate (TWR) from univariate glmer-models controlling for the effect of hunting unit. T/Z-values are included in addition to p-values and R²m. Statistical significant ($p < 0.050$) effects are marked bold, whereas variables with strong support ($p < 0.100$) that were included in the multivariate models are marked by italic font. Parameter estimates for twinning rate are at the logit-scale. All explanatory variables are square-root transformed. $N_{\text{calves}} = 2571$, $N_{\text{yearling♀}} = 398$, $N_{\text{yearling♂}} = 746$, $N_{\text{hunting unit}} = 74$, $N_{\text{year}} = 11$.

Explanatory variable	LHT	$\beta \pm \text{SE}$	t/z-value	p-value	R ² m
Agricultural area	CCM	8.456 \pm 2.419	3.50	<0.001	0.023
	YCM ♀	21.878 \pm 5.576	3.92	<0.001	0.066
	YCM ♂	22.615 \pm 3.932	5.75	<0.001	0.069
	TWR	2.461 \pm 0.312	7.90	<0.001	0.068
Forest	CCM	-2.439 \pm 4.432	-0.55	0.584	<0.001
	YCM ♀	3.723 \pm 11.815	0.32	0.753	<0.001
	YBM ♂	-0.867 \pm 7.979	-0.11	0.914	<0.001
	TWR	0.589 \pm 0.776	0.76	0.448	0.001
Barren land and bog	CCM	-4.028 \pm 2.637	-1.53	0.131	0.005
	YCM ♀	-17.317 \pm 6.517	-2.66	0.010	0.031
	YCM ♂	-15.392 \pm 4.560	-3.38	0.001	0.028
	TWR	-2.072 \pm 0.399	-5.20	<0.001	0.045
Deciduous and mixed forest	CCM	10.811 \pm 5.915	1.83	0.072	0.006
	YCM ♀	26.735 \pm 15.315	1.75	0.086	0.014
	YCM ♂	36.710 \pm 10.510	3.49	<0.001	0.030
	TWR	4.474 \pm 1.000	4.52	<0.001	0.036
Mixed coniferous and pine forest	CCM	-8.548 \pm 4.605	-1.86	0.067	0.006
	YCM ♀	7.764 \pm 12.010	0.65	0.520	0.002
	YCM ♂	-2.237 \pm 9.122	-0.25	0.807	<0.001
	TWR	0.894 \pm 0.845	1.06	0.290	0.003
Spruce dominated forest	CCM	1.239 \pm 2.715	0.46	0.649	<0.001
	YCM ♀	5.035 \pm 7.527	0.67	0.505	0.002
	YCM ♂	5.922 \pm 5.121	1.16	0.251	0.003
	TWR	1.050 \pm 0.491	2.14	0.033	0.010
Impediment and low forest productivity class	CCM	-8.315 \pm 3.106	-2.68	0.009	0.013
	YCM ♀	-8.663 \pm 8.047	-1.08	0.286	0.006
	YCM ♂	-11.845 \pm 5.809	-2.04	0.045	0.011
	TWR	-1.113 \pm 0.545	-2.04	0.041	0.009
Intermediate and high productivity classes	CCM	3.537 \pm 2.782	1.27	0.207	0.003
	YCM ♀	5.711 \pm 7.580	0.75	0.453	0.002
	YCM ♂	8.957 \pm 5.206	1.72	0.089	0.007
	TWR	1.141 \pm 0.485	2.35	0.019	0.013
Elevation	CCM	-1.606 \pm 1.274	-1.26	0.212	0.003
	YCM ♀	-7.209 \pm 3.120	-2.31	0.024	0.024
	YCM ♂	-8.115 \pm 2.170	-3.74	<0.001	0.033
	TWR	-1.103 \pm 0.184	-5.98	<0.001	0.052
TWR	CCM	1.923 \pm 1.081	1.78	0.075	0.002
YCM ♀	TWR	0.720 \pm 0.152	4.74	<0.001	0.037

Table A.2: AIC_c- based ranking of models explaining the spatial variation for the life history traits (LHT): calf carcass mass (CCM), female yearling carcass mass (YCM ♀), male yearling carcass mass (YCM ♂) and twinning rate (TWR) using multivariate lmer-models for carcass mass, controlling for the effect of hunting unit and year, and multivariate glmer-models for TWR controlling for the effect of hunting unit, with the significant variables found in Table 1. Variables included in the global model for each LHT are shaded grey and the variables included in the candidate model are indicated by an x. ΔAIC_c indicate the difference between the best model (model 1) and the candidate models. Only the models with $\Delta AIC_c < 2$ are presented. All explanatory variables are square-root transformed.

Model	LHT	Agricultural areas	Barren land and bog forest	Deciduous and mixed forest	Mixed coniferous and pine forest	Spruce dominated forest	Impediment and low productivity class	Intermediate and high productivity classes	Elevation	YCM ♂	TWR	K	ΔAIC_c	AIC _c weight	R ² m
1	CCM	x			x							6	0.00	0.156	0.028
2	CCM	x			x		x					7	0.70	0.110	0.029
3	CCM	x										5	0.87	0.101	0.024
4	CCM	x					x					6	1.47	0.075	0.026
5	CCM	x									x	6	1.80	0.063	0.024
6	CCM	x			x		x					7	1.98	0.058	0.028
1	YCM ♀	x							x			6	0.00	0.264	0.077
2	YCM ♀	x										5	0.72	0.184	0.066
3	YCM ♀	x	x						x			7	1.09	1.153	0.082
4	YCM ♀	x		x								6	1.57	1.120	0.073
5	YCM ♀	x		x					x			7	1.99	0.098	0.078
1	YCM ♂	x										5	0.00	0.114	0.069
2	YCM ♂	x							x			6	0.46	0.091	0.072
3	YCM ♂	x	x									6	0.91	0.072	0.071
4	YCM ♂	x						x	x			6	1.11	0.066	0.072
5	YCM ♂	x		x					x			7	1.54	0.053	0.074
6	YCM ♂	x					x		x			7	1.55	0.053	0.073
7	YCM ♂	x					x					6	1.73	0.048	0.069
1	TWR	x					x			x		5	0.00	0.062	0.083
2	TWR	x				x	x	x		x		7	0.89	0.040	0.084
3	TWR	x					x	x		x		6	1.01	0.038	0.082
4	TWR	x		x		x	x	x		x		8	1.34	0.032	0.084
5	TWR	x		x		x		x		x		7	1.47	0.030	0.081
6	TWR	x		x			x	x		x		7	1.55	0.029	0.082
7	TWR	x		x			x			x		6	1.61	0.028	0.084
8	TWR	x				x	x			x		6	1.61	0.028	0.079
9	TWR	x					x	x	x	x		7	1.62	0.028	0.082
10	TWR	x					x		x	x		6	1.86	0.025	0.084
11	TWR	x				x	x			x		6	1.99	0.023	0.083

Table A.3: Parameter estimates ($\beta \pm \text{SE}$) from the most parsimonious multivariate lmer models based on AIC_c -values explaining spatial variation in calf carcass mass (CCM), female yearling carcass mass ($\text{YCM}_\text{♀}$), male yearling carcass mass ($\text{YCM}_\text{♂}$), while controlling for the effect hunting unit and year. And parameter estimates ($\beta \pm \text{SE}$) from the most parsimonious multivariate glmer model explaining variation in twinning rate (TWR) with hunting unit as random factor (Table A.3). All the explanatory variables are square root transformed. Estimates of twinning rate is on logit-scale. $N_{\text{calves}} = 2571$, $N_{\text{YCM}_\text{♀}} = 398$, $N_{\text{YCM}_\text{♂}} = 746$, $N_{\text{hunting unit}} = 74$, $N_{\text{year}} = 11$.

	$\beta \pm \text{SE}$	t/z-value	p-value
CCM			
Intercept	57.882 \pm 1.800	32.15	<0.001
Agricultural areas	8.133 \pm 2.404	3.38	0.001
Mixed coniferous and pine forest	-7.360 \pm 4.359	-1.69	0.095
YCM_♀			
Intercept	93.949 \pm 11.787	7.97	<0.001
Agricultural areas	36.214 \pm 10.211	3.55	<0.001
Elevation	8.996 \pm 5.372	1.68	0.098
YCM_♂			
Intercept	113.004 \pm 1.633	69.22	<0.001
Agricultural areas	22.615 \pm 3.932	5.75	<0.001
TWR			
Intercept	-5.974 \pm 1.390	-4.30	<0.001
Agricultural areas	2.576 \pm 0.405	6.36	<0.001
Impediment and low productivity class	0.995 \pm 0.488	2.04	0.041
YCM_♂	0.306 \pm 0.130	2.35	0.019

Table A.4: Mean values (\pm standard error) for the life history traits (LHT): calf carcass mass (CCM) (kg), yearling female carcass mass (YCM ♀) (kg), yearling male carcass mass (YCM ♂) (kg) and twinning rate (TWR)(twin producing females of all calf-producing females) per hunting unit. Hunting unit code with the first four digits ‘1711’ are hunting units located in Meråker, and ‘1714’ are hunting units located in Stjørdal. $N_{\text{calves}}=2571$, $N_{\text{yearling♀}}=398$, $N_{\text{yearling♂}}=746$, $N_{\text{hunting unit}} = 74$, $N_{\text{year}} = 11$.

Hunting unit	CCM	YCM ♀	YCM ♂	TWR
1711J0001	56.45 \pm 4.249	NA	102.77 \pm 10.102	NA
1711J0002	54.26 \pm 6.157	115.46 \pm 15.959	105.25 \pm 15.626	0.17 \pm 0.075
1711J0003	60.83 \pm 6.121	130.82 \pm 22.540	116.64 \pm 14.241	0.15 \pm 0.051
1711J0006	60.13 \pm 6.362	110.39 \pm 22.486	118.13 \pm 14.978	0.15 \pm 0.076
1711J0007	52.27 \pm 5.811	103.80 \pm 20.974	123.04 \pm 14.501	0.12 \pm 0.035
1711J0008	57.38 \pm 5.937	112.39 \pm 22.476	111.55 \pm 16.955	0.18 \pm 0.068
1711J0009	61.33 \pm 5.764	111.96 \pm 20.976	113.33 \pm 13.705	0.12 \pm 0.039
1711J0010	56.15 \pm 6.157	NA	131.23 \pm 16.988	NA
1711J0011	55.69 \pm 5.779	118.30 \pm 20.130	122.31 \pm 15.655	0.07 \pm 0.019
1711J0012	58.94 \pm 6.537	NA	109.53 \pm 17.039	NA
1711J0013	53.34 \pm 6.034	95.19 \pm 22.540	114.05 \pm 13.690	0.07 \pm 0.049
1711J0014	56.51 \pm 5.791	109.92 \pm 20.658	106.83 \pm 13.606	0.14 \pm 0.061
1711J0015	57.71 \pm 5.639	111.64 \pm 19.847	116.62 \pm 13.125	0.10 \pm 0.017
1711J0017	60.00 \pm 5.924	122.77 \pm 21.020	118.19 \pm 13.835	0.21 \pm 0.046
1711J0018	56.72 \pm 6.532	NA	126.66 \pm 16.942	NA
1711J0019	62.06 \pm 5.754	135.32 \pm 20.608	135.98 \pm 13.992	0.34 \pm 0.044
1711J0020	62.03 \pm 5.746	111.90 \pm 20.643	123.86 \pm 13.988	0.24 \pm 0.061
1711J0021	57.72 \pm 5.755	123.46 \pm 20.424	106.76 \pm 14.197	0.24 \pm 0.057
1714J0001	51.88 \pm 5.923	111.39 \pm 20.677	122.12 \pm 13.506	0.30 \pm 0.087
1714J0002	52.74 \pm 5.629	120.27 \pm 19.519	129.81 \pm 12.899	0.52 \pm 0.036
1714J0003	54.62 \pm 5.841	118.19 \pm 20.667	116.31 \pm 13.278	0.35 \pm 0.075
1714J0005	55.03 \pm 5.834	116.23 \pm 20.273	122.27 \pm 13.697	0.39 \pm 0.047
1714J0006	60.14 \pm 5.726	116.70 \pm 20.446	125.65 \pm 13.133	0.27 \pm 0.049
1714J0007	52.44 \pm 5.895	112.95 \pm 20.608	109.67 \pm 13.709	0.25 \pm 0.080
1714J0008	50.87 \pm 6.088	108.41 \pm 20.940	120.59 \pm 14.224	0.18 \pm 0.042
1714J0009	58.81 \pm 5.969	119.70 \pm 21.435	112.43 \pm 13.691	0.19 \pm 0.098
1714J0010	54.24 \pm 6.532	104.75 \pm 22.540	109.09 \pm 20.445	0.06 \pm 0.046
1714J0011	47.43 \pm 5.871	105.90 \pm 20.442	110.88 \pm 14.964	0.19 \pm 0.051
1714J0012	53.54 \pm 5.989	112.08 \pm 20.622	109.80 \pm 13.593	0.14 \pm 0.050
1714J0013	47.70 \pm 6.244	120.33 \pm 25.371	98.96 \pm 15.645	0.03 \pm 0.022
1714J0014	47.38 \pm 6.440	118.55 \pm 21.477	131.59 \pm 14.224	0.05 \pm 0.031
1714J0015	60.99 \pm 5.850	125.97 \pm 20.666	124.10 \pm 13.696	0.46 \pm 0.037
1714J0016	61.74 \pm 8.146	137.44 \pm 21.512	125.76 \pm 15.652	0.45 \pm 0.112
1714J0017	60.33 \pm 5.841	143.62 \pm 22.539	137.80 \pm 14.221	0.41 \pm 0.092
1714J0018	59.02 \pm 5.715	120.82 \pm 19.865	123.43 \pm 12.974	0.35 \pm 0.049
1714J0019	65.14 \pm 5.700	128.60 \pm 19.921	130.30 \pm 13.503	0.32 \pm 0.053
1714J0020	59.14 \pm 5.669	129.05 \pm 19.713	121.82 \pm 12.862	0.27 \pm 0.043
1714J0021	56.14 \pm 5.721	127.56 \pm 19.982	121.53 \pm 12.981	0.18 \pm 0.045
1714J0022	57.65 \pm 5.882	135.01 \pm 20.108	125.16 \pm 13.430	0.28 \pm 0.047
1714J0024	66.32 \pm 5.907	140.27 \pm 20.248	125.03 \pm 13.511	0.33 \pm 0.041
1714J0025	62.33 \pm 5.824	118.42 \pm 21.537	109.49 \pm 13.376	0.30 \pm 0.051
1714J0026	65.76 \pm 5.862	123.48 \pm 21.517	122.00 \pm 13.979	0.30 \pm 0.047

Hunting unit	CCM	YCM ♀	YCM ♂	TWR
1714J0027	57.95 ± 5.989	NA	121.35 ± 14.225	NA
1714J0028	57.77 ± 5.685	116.98 ± 20.248	124.00 ± 13.131	0.18 ± 0.050
1714J0030	61.06 ± 5.817	118.39 ± 20.977	133.30 ± 15.654	0.42 ± 0.081
1714J0031	65.09 ± 5.692	139.42 ± 20.153	127.04 ± 13.140	0.40 ± 0.047
1714J0032	62.35 ± 6.156	115.09 ± 20.427	129.97 ± 14.211	0.05 ± 0.028
1714J0033	65.31 ± 5.860	145.70 ± 25.263	124.09 ± 13.588	0.35 ± 0.048
1714J0034	62.09 ± 5.784	128.76 ± 19.976	140.13 ± 13.825	0.45 ± 0.078
1714J0035	59.75 ± 7.221	125.28 ± 25.361	112.91 ± 15.644	0.02 ± 0.020
1714J0036	61.77 ± 5.792	127.80 ± 20.643	130.50 ± 14.205	0.27 ± 0.044
1714J0037	51.33 ± 5.697	100.65 ± 20.045	109.95 ± 12.982	0.06 ± 0.025
1714J0038	52.73 ± 5.862	114.71 ± 21.513	107.36 ± 13.514	0.19 ± 0.042
1714J0039	56.11 ± 5.922	108.91 ± 21.471	118.34 ± 13.381	0.13 ± 0.035
1714J0040	62.71 ± 6.120	107.14 ± 25.395	114.24 ± 20.410	0.23 ± 0.065
1714J0041	58.61 ± 5.920	108.56 ± 20.268	111.13 ± 13.831	0.10 ± 0.031
1714J0042	53.84 ± 5.742	108.39 ± 19.918	113.47 ± 13.059	0.11 ± 0.032
1714J0043	59.67 ± 5.699	123.47 ± 19.987	115.72 ± 13.143	0.08 ± 0.019
1714J0044	51.34 ± 5.797	107.50 ± 20.042	106.84 ± 13.322	0.09 ± 0.038
1714J0045	48.00 ± 6.254	115.93 ± 25.371	111.30 ± 14.968	0.18 ± 0.110
1714J0046	55.60 ± 5.803	111.86 ± 20.121	113.92 ± 13.434	0.24 ± 0.037
1714J0047	51.26 ± 5.907	110.69 ± 20.644	109.28 ± 13.322	0.13 ± 0.035
1714J0048	53.37 ± 5.625	115.42 ± 19.590	115.07 ± 13.088	0.15 ± 0.026
1714J0049	60.36 ± 5.791	114.02 ± 20.589	122.22 ± 13.508	0.10 ± 0.037
1714J0050	59.74 ± 5.907	128.89 ± 21.480	122.36 ± 13.600	0.11 ± 0.042
1714J0051	55.08 ± 5.657	121.09 ± 20.067	118.06 ± 13.073	0.25 ± 0.037
1714J0052	53.43 ± 6.363	122.25 ± 21.517	112.75 ± 14.942	0.17 ± 0.099
1714J0053	55.20 ± 5.952	131.76 ± 21.511	117.74 ± 13.990	0.29 ± 0.061
1714J0054	58.72 ± 5.709	120.77 ± 20.635	122.83 ± 13.599	0.23 ± 0.034
1714J0055	59.97 ± 6.121	152.30 ± 22.543	135.42 ± 16.960	0.24 ± 0.089
1714J0117	61.72 ± 5.935	126.68 ± 20.606	111.30 ± 13.433	0.12 ± 0.059
1714J0118	60.74 ± 6.973	NA	NA	NA
1714J0119	60.72 ± 6.445	120.66 ± 21.473	121.65 ± 14.988	0.21 ± 0.066
1714J0121	59.14 ± 6.369	118.09 ± 22.477	110.79 ± 20.439	0.27 ± 0.067

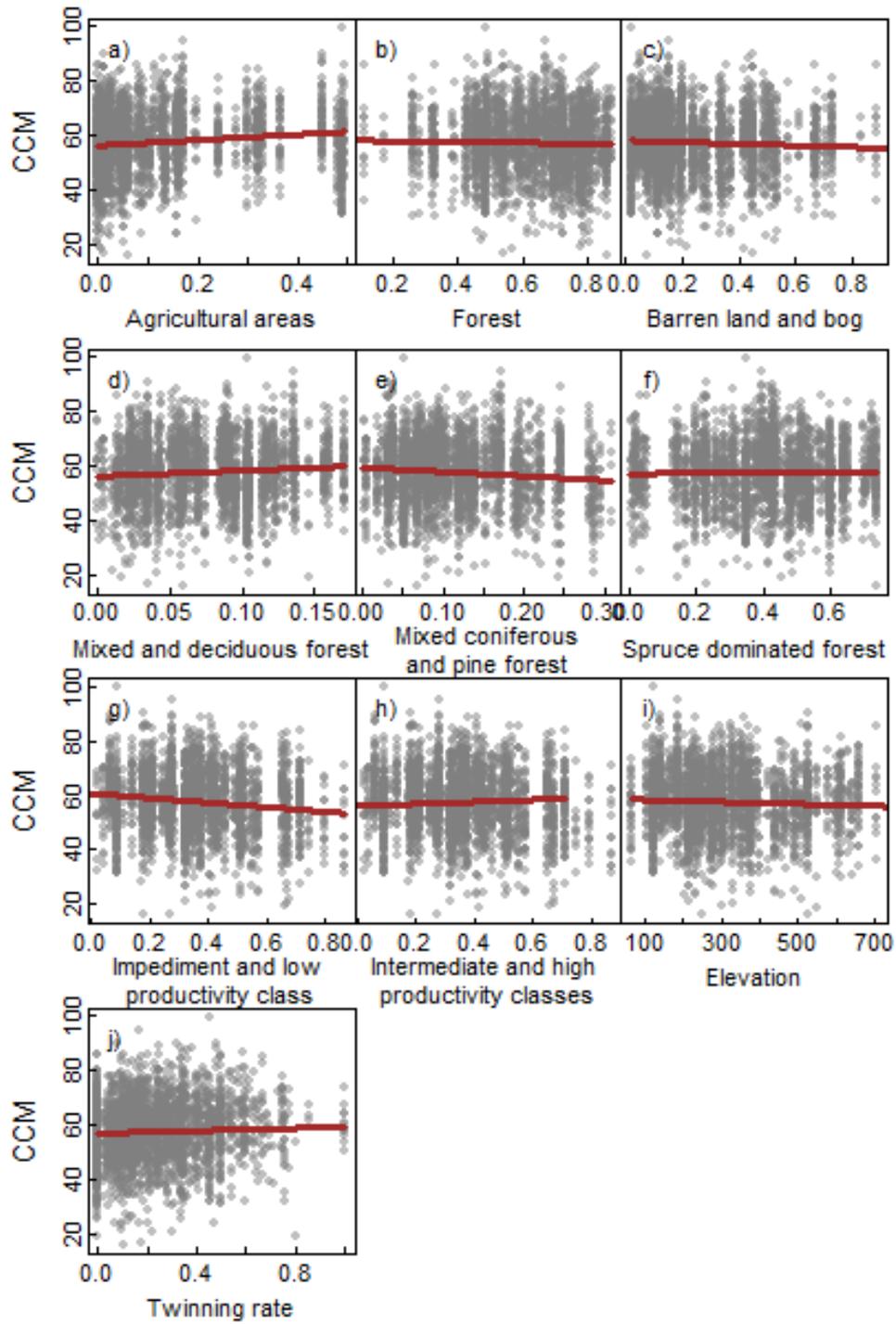


Fig. A.1: The relationships between calf carcass mass (CCM) and the proportion of habitat variables, mean elevation and twinning rate in the hunting units in Stjørdal and Meråker.

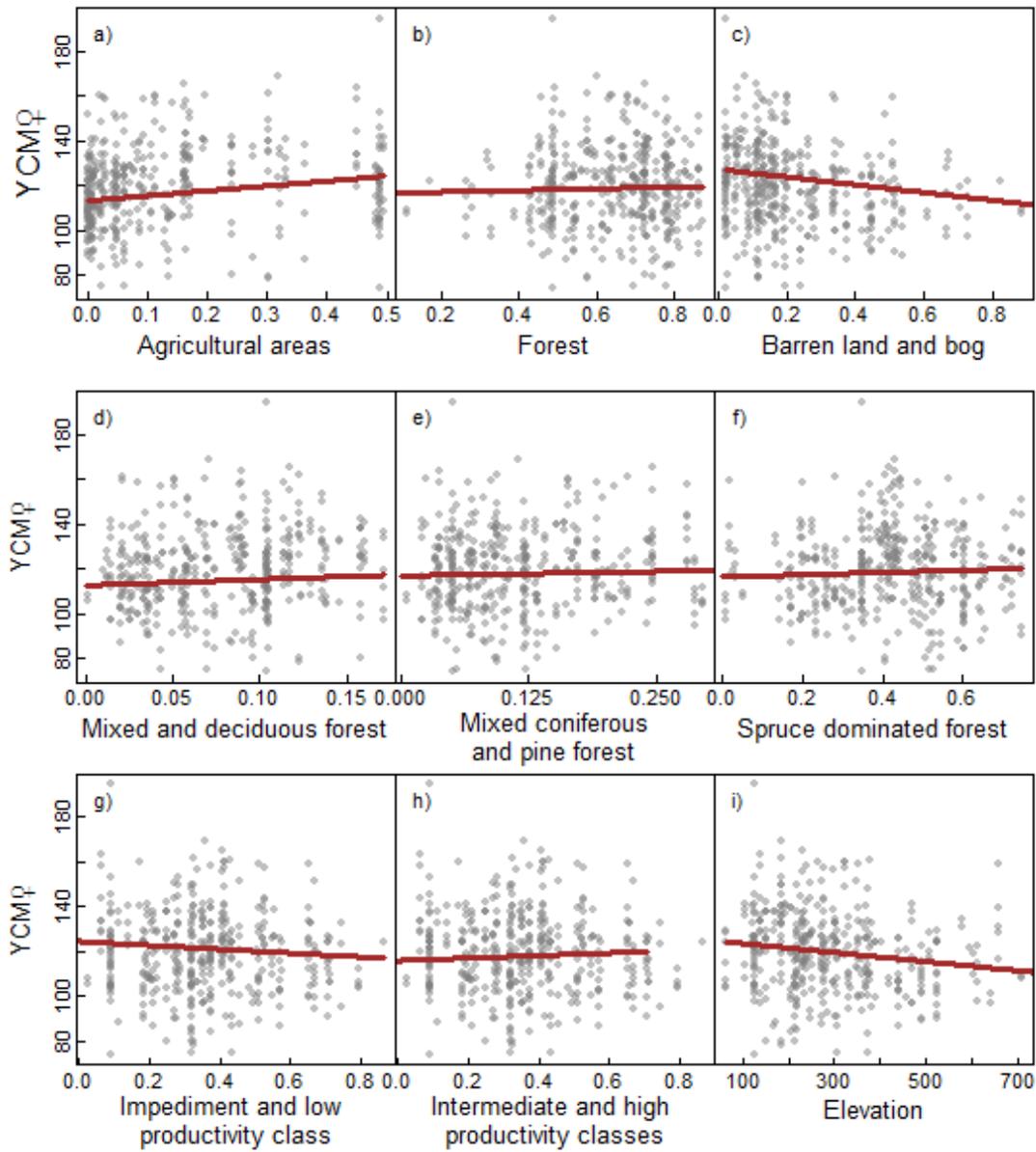


Fig. A.2: The relationships between female yearling carcass mass ($YCM_{\text{♀}}$) and the proportion of habitat variables and mean elevation in the hunting units in Stjørdal and Meråker.

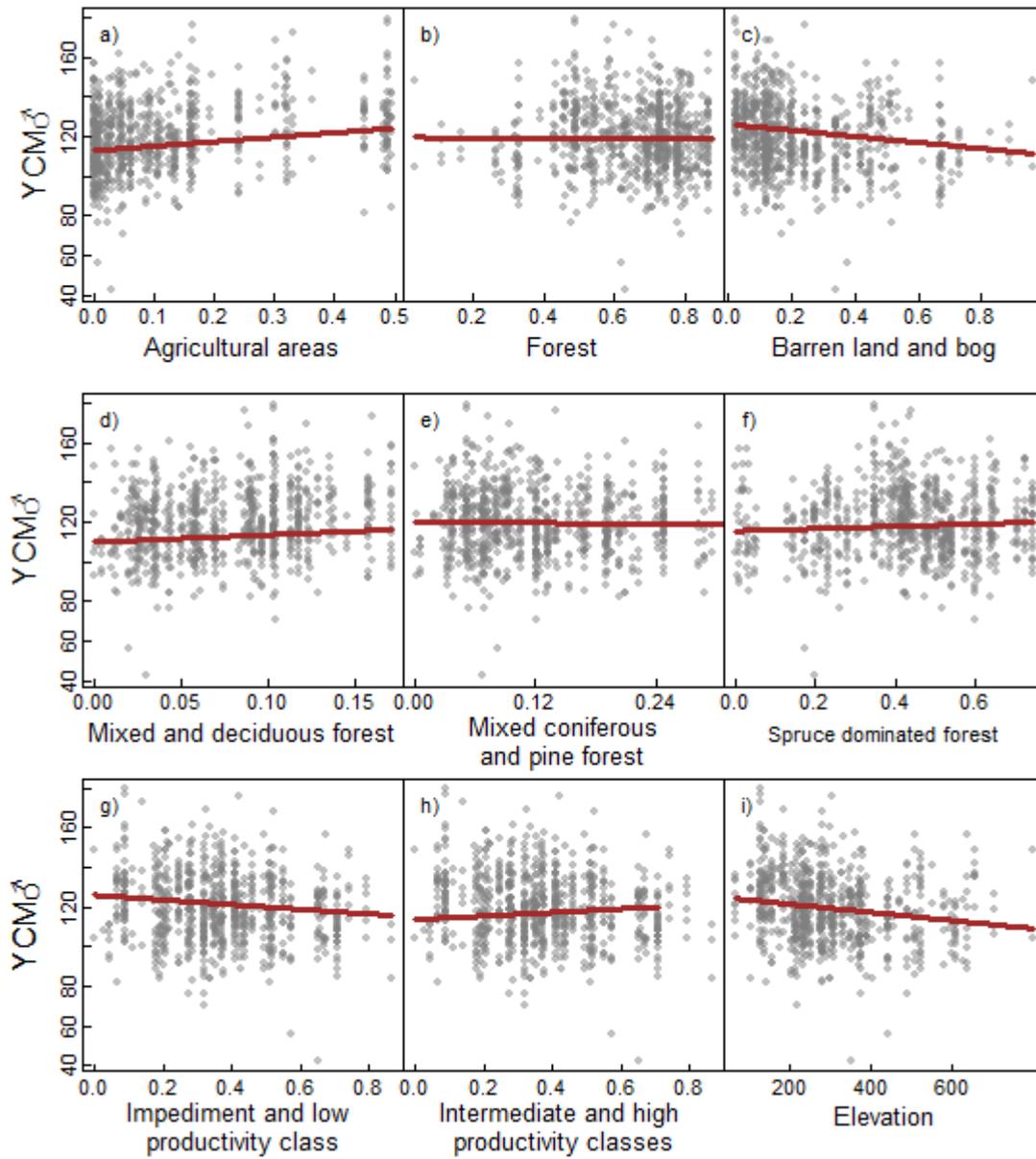


Fig. A.3: The relationships between male yearling carcass mass ($YCM_{\text{♂}}$) and the proportion of habitat variables and mean elevation in the hunting units in Stjørdal and Meråker.

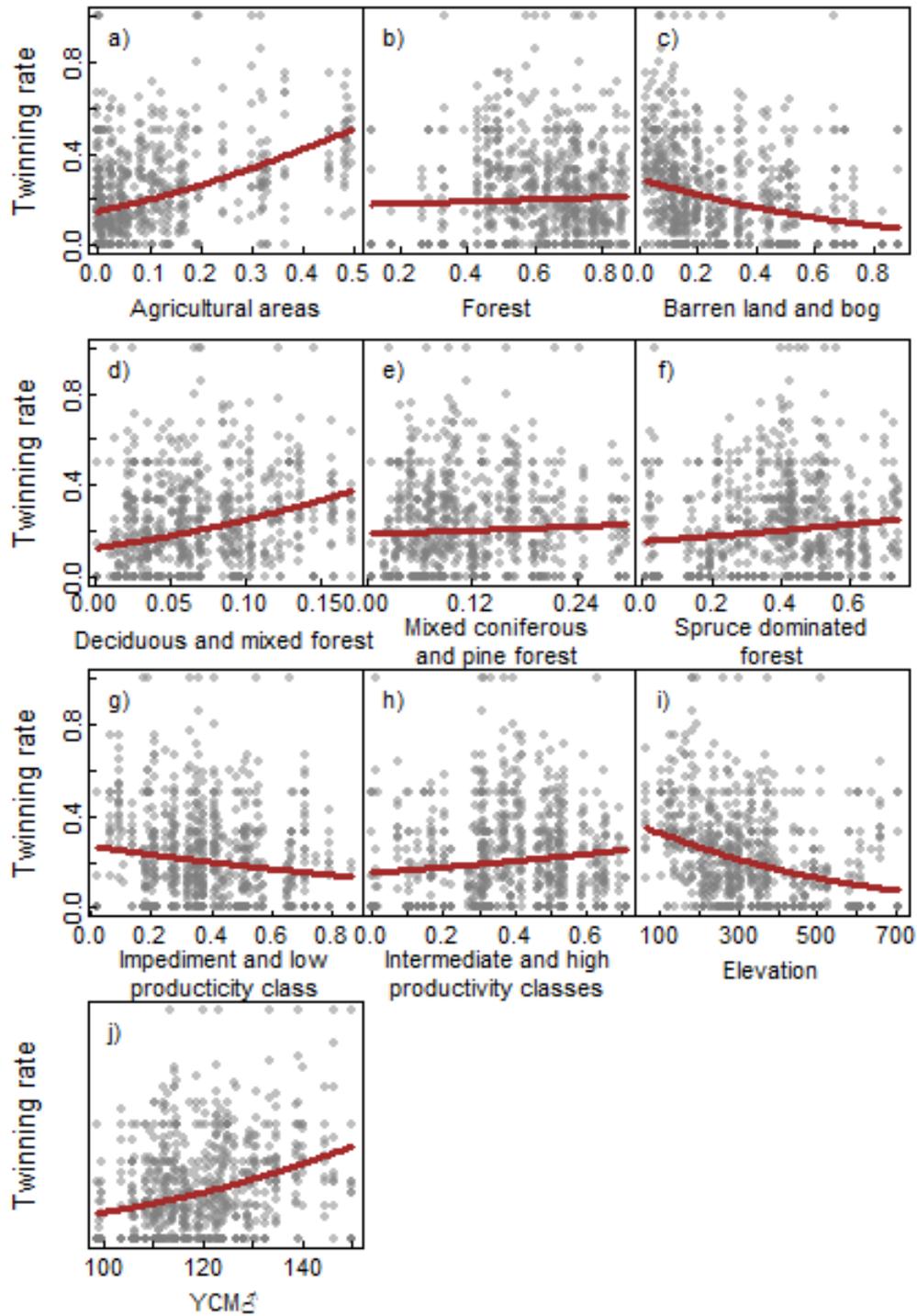


Fig. A.4: The relationships between twinning rate and the proportion of habitat variables, mean elevation and female yearling carcass mass ($YCM_{\text{♀}}$) in the hunting units in Stjørdal and Meråker.

Table A.5: Matrix with Pearson's correlation coefficients (N=74 hunting units) for the explanatory variables used to explain spatial variation in life history traits in moose. Abbreviations: YCM_♀ = female yearling carcass mass, TWR = twinning rate.

	Forest	Barren land and bog	Deciduous and mixed forest	Mixed coniferous and pine forest	Spruce dominated forest	Impediment and low productivity class	Intermediate and high productivity classes	Elevation	YCM _♀	TWR
Agricultural areas	-0.03	-0.59	0.62	-0.20	0.14	-0.54	0.32	-0.73	0.40	0.74
Forest		-0.79	0.29	0.32	0.83	0.21	0.75	-0.56	0.10	0.07
Barren land and bog			-0.62	-0.14	-0.76	0.17	-0.80	0.90	-0.33	-0.52
Deciduous and mixed forest				0.03	0.38	-0.29	0.56	-0.71	0.14	0.42
Mixed coniferous and pine forest					0.16	0.71	-0.11	-0.13	0.04	0.02
Spruce dominated forest						-0.01	0.87	-0.66	0.16	0.18
Impediment and low productivity class							-0.29	0.26	-0.13	-0.27
Intermediate and high productivity classes								-0.71	0.14	0.20
Elevation									-0.31	-0.57
YCM_♂										0.52